The Basal Sclerites of the Leg in Insects.

By

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With Plate 1–3.

The various and conflicting theories concerning the comparison of the parts of an insect's leg with those of a crustacean and other arthropods, are of too highly speculative a nature to make their discussion profitable, in the present state of our knowledge concerning them. The first part of the present paper is therefore limited to the description of the sclerites themselves, and the interpretation of the modifications met with in different insects. In the second part of the paper, the above mentioned theories are briefly reviewed, without attempting to discuss their relative merits, while more consideration is given to the discussion of the views of other investigators concerning the homologies of the sclerites in various insects, and the points wherein their views differ from those herein expressed.

In order to avoid the influence of any preconceived ideas concerning the homologies of the sclerites, or the considering of the evidence from a biased standpoint, it has seemed advisable that two persons should collaborate in the preparation of the present

paper. For the sake of uniformity, however, all of the drawings have been made by Mr. Hasey alone.

When the two writers of the present paper were not in accord as to the interpretation of the sclerites, the opinions of both have been given: otherwise, the views herein expressed, are those which have appealed to both alike.

The articulation of the leg.

In comparing together the sclerites of different insects, it is necessary first to establish certain fixed points, or "landmarks", whose position is constant throughout the entire series. The homologies of the various sclerites may then be readily determined by the relation they bear to the landmarks in question.

Four such landmarks of importance in the study of the basal sclerites of the leg, are as follows. 1. The pleural suture (Figs. 2, 3, 4, 8, etc., *g*) extending from the top to the bottom of the pleural plate, and separating the episternum, *es*, from the epimeron, *em*. It is continued downward into the coxa as the coxal suture, *l*, which divides the coxa into an anterior and posterior region, *vc* and *me*. 2. The pleural fulcrum of the coxa (Fig. 9a), or projection of the pleural plate at the bottom of the pleural suture, serving as a pivot, or fulcrum, in the movements of the coxa. 3. The apex of the trochantin (Fig. 9b), which may likewise serve as a pivot, or fulcrum, in the movements of the coxa, when the trochantin is immovably united with the lower portion of the pleural plate; but when the trochantin, or its terminal portion, remains detached to form a distinct, movable plate, it is probable that it then acts merely as a point of attachment for certain muscles moving the coxa. 4. The sternal fulcrum of the coxa (Fig. 9c), or projection of the sternal region forming a pivot, or fulcrum, in the movements of the coxa. This projection is usually absent in the lower insects, but is well developed in the higher forms, such as the Neuroptera, Trichoptera, Lepidoptera, Diptera, etc.

The trochantin.

One of the most important of the articulatory sclerites at the base of the leg, is the trochantin, or trochantinus. Since this sclerite has been the subject of such diverse interpretations by different investigators, it may be of some interest to establish its true identity. In its most characteristic form, the trochantin occurs

as a triangular plate *tn* (Figs. 2. 3, and 22) divided by an oblique suture, into an anterior and posterior region (Figs. 2 and 22, *at* and *pt*). The anterior region, *at*, is the one chiefly concerned in the formation of the articulation with the coxa, the posterior region, *pt*, being usually, though not always, situated slightly back of this point.

The true trochantin is always situated in front of the pleural fulcrum of the coxa, and a portion of the episternum (or its homologue) always intervenes between it and the pleural suture, although this is not always evident until the specimen has been boiled in caustic potash, and the parts have been spread apart. In some instances, the trochantin is separated from the lower portion of the pleural plate by a membranous area, or by a suture. while in other cases, it is more or less completely united with the lower portion of the pleural plate.

The following modifications of the typical form of the trochantin are met with in various insects. In the mesothorax of the earwig (Fig. 19) there are two distinct plates, *at* and *pt*, which may correspond, in a general way, to the anterior and posterior regions, *at* and *pt*, marked off by the oblique suture in the typical trochantin (Figs. 22, *2* and *3*). One of the writers of the present paper, however, considers that the sclerite *at* of Fig. 19, may represent the entire trochantin, while the plate *pt* may be a new formation, as is the case with the small plate *jc* of Figs. 19 and 22.

In the prothorax of the roaches or Blattoidea (and in the prothorax of such insects as the Phasmoidea, Isoptera, etc., which are closely related to them) the basal portion of the trochantin, *bt* (Fig. 1), unites with the lower portion of the pleural plate, while the terminal portion of the trochantin, *tnl*, becomes detached to form a distinct plate, designated as the trochantinelle, in previous writings. The small plate *tnl*, is usually incorrectly designated as the entire trochantin, while the basal portion, *bt*, is mistaken for a portion of the episternum The basal region, *bt*, however, is separated from the episternum by a well marked suture, in many roaches, and a portion of the episternum, *es*, intervenes between it and the pleural suture, as is the case in the typical condition of the trochantin; so that it is difficult to understand how such a mistaken conception of the nature of the sclerite in question, could have arisen.

In attempting to homologize the parts of the region *ptn* of *Mantispa* and *Corydalis* (Figs. 8 and 13) with those of the roach (Figs. 1 and 2), the following points should be observed. The pro-

jecting region *tnl*, of Figs. 8 and 9, is evidently a portion of the trochantin, since it forms one of the points of articulation with the coxa, and is divided by an oblique suture, as in the trochantin of the roach (Figs. 1 and 2, *tn*). On the other hand, the region *ac* of Figs. 8 and 9, is not a portion of the true trochantin (*tn*, of Figs. 2, 3, 22, etc.) for the typical trochantin is never connected with the sternal region. On this account, the region *ac* of Figs. 8 and 9 must correspond to the narrow marginal region *ac*, of Figs. 1 and 2. Furthermore, since the episternum (*es*, of Figs. 1 and 2) always extends from the top to the bottom of the pleural plate, along the pleural suture, *g*, that portion of the region *ptn* of Figs. 8 and 9, bordering upon the pleural suture, *g*, must be the lower portion of the episternum. In other words, if the suture marking off the region *ac* of Figs. 1 and 2, be thought of as prolonged above the base of the trochantin until it meets (or almost meets) the pleural suture *g*, and if the suture between the trochantin and the lower portion of the episternum were obliterated, we would have a compound sclerite homologous with the composite region designated as *ptn* in Figs. 8, 9, and 13. This composite sclerite *ptn*, is therefore made up of the region *ac*, the trochantin, and the lower portion of the episternum, and therefore cannot be designated as the trochantin alone. It has been designated as the "pleurotrochantin" in a previous paper (Crampton, 1914) and this term will be retained in the present paper.

Some investigators regard the region *ptn* (Figs. 8 and 13) as the trochantin alone (Figs. 1, 2, 3, and 22, *tn*). They are consequently forced to make the unwarrented assumption that the small region *aes* of Figs. 13 and 8, represents the entire episternum *es*, of Figs. 1, 2, 3, etc.! The episternum (or its homologue) however, always extends from the top to the bottom of the pleural plate, along the pleural suture. On the other hand, it is not uncommon for both episternum and epimeron to become divided into an upper and lower region, by the formation of secondary sutures, as is the case in *Mantispa* (Fig. 13). And lastly, in the roach *Ischnoptera* (Fig. 2) the sclerite *es*, which everyone admits is the true episternum, is marked off into an upper region *aes* (Fig. 2), in every way homologous with the region *aes* of Figs. 8 and 13. These facts and a study of the musculature, can lead to no other conclusion but that the region *aes* of Figs. 8 and 13, is merely the upper portion of the episternum, called the anepisternum, while the region *ptn* of Figs. 8 and 13, is a composite sclerite, composed of the lower

portion of the episternum, together with the trochantin, and the narrow marginal region *ac* (Figs. 1, 2 etc.).

It is apparent from the foregoing discussion, that the trochantin may unite with the lower portion of the pleural plate, to form a compound sclerite *ptn* (Figs. 13 and 8) marked off by a well defined suture extending to the pleural suture *g*. If this suture (marking off the region *ptn*) were continued backward beyond the pleural suture, it would demark a region composed of the trochantin, etc., together with the lower portion of the pleural plate, and would correspond roughly to the combined sclerites *ptn* and *hem* of Fig. 13. If this composite region, consisting of the trochantin and the lower portion of the pleural plate, were to become detached to form a distinct plate, we would have a condition similar to that represented in the plate designated as *pst* (Fig. 21) in the prothorax of the stonefly *Perla*. In the meso- and metathorax of this insect, the base of the trochantin is completely and indistinguishably fused with the lower portion of the pleural plate, so that it is not surprising that the lower portion of the pleural region would remain united with the trochantin, when the latter became detached, in the prothorax, to form the composite region *pst*. The location of the plate *pst* (Fig. 21) with reference to the pleural coxal fulcrum (at the bottom of the pleural suture) clearly shows that this plate comprises an area of much greater extent (posteriorly) then the trochantin (*tn* of Figs. 2, 3, and 22) alone. Furthermore, the fact that the composite sclerite *pst* (Fig. 21) contains the lower portion of the pleural suture (which is not continued down into the coxa, in this case) clearly shows that the lower portion of the pleural region has become detached from the remainder, and has united with the trochantin to form the plate *pst*. We have therefore designated the plate *pst* of Fig. 21, as the "pseudo-trochantin", to indicate that it is not strictly homologous with the trochantin alone (i. e. *tn*, of Figs. 2, 3, and 22).

It is very probable that the plate *pst* of Fig. 21, is homologous with the plate labeled *pst* in the thorax of *Eosentomon* (Fig. 20). If this is true, the plate usually designated as the trochantin alone, in the apterygote insects, is in reality a "pseudo-trochantin".

The sclerites *ac* and *sc*, found in the metathorax of the grasshopper *Dissosteira* (Fig. 16) are sometimes mistaken for the trochantin; but the sclerite designated as *ac* in Fig. 16 is homologous with the sclerite *ac* of Fig. 2, called the antecoxal piece, or antecoxale, while the sclerite *sc* of Fig. 16 is a new formation marked off in the

sternal region, by the formation of secondary sutures, not present in other insects, and is therefore an entirely different plate from the trochantin, which is frequently present in certain grasshoppers. Both of the sclerites *ac* and *sc*, which occur as distinct sclerites in the metathorax of the grasshopper (Fig. 16), are included in the circular region *per*, which forms a ring above the base of the coxa, in the mesothorax of this insect (Fig. 17).

Near the base of the coxa there occurs in certain insects, a small sclerite *jc* (Figs. 1, 19, and 22) which frequently bears an internal process to which are attached certain of the muscles which move the coxa. In the meso- and metathorax of the roach *Periplaneta*, it is situated close to the margin of the coxa, and in most insects, it is indistinguishably united with the coxa. It is always small and unimportant.

The coxa.

In the prothorax of the Plecoptera (Fig. 21) and in the meso- and metathorax of the Myrientomata (Fig. 20), the coxa *cx* is reduced to a rather narrow ring, being broader than long in these insects. In the Thysanura (Fig. 18) on the other hand, and in many winged insects, the coxa is longer than broad. In certain beetles, the posterior coxae are transversely elongate and extremely flat (Fig. 24) and being set in the coxal cavities, they lie in the same plane with the sternal region, and were frequently mistaken for a portion of the sternum by certain of the earlier entomologists.

In the meso- and metathorax of certain Thysanura, such as *Machilis* (Fig. 18), the coxa bears a styliform appendage *stg* strongly suggestive of the so-called styli of Myriopods. These styliform appendages, however, bear no relation to the meron, or posterior region of the coxa, presently to be described, although some writers have sought to homologize the two.

The coxa is not divided into an anterior and posterior subdivision in the apterygote, or primitively wingless insects, nor is it so divided in any of the larvae of winged insects examined by the writers. Certain adult pterygote insects have also preserved the primitive undivided condition in the coxae of all of the thoracic segments, and in those segments which do not bear a functional wing (such as the prothorax of all insects, and the mesothorax of the Diptera) the coxa is always undivided.

In the meso- and metathorax of many winged insects, the coxa

is "dicoxal", or is divided into an anterior and posterior region *vc* and *me* (Figs. 2, 3, 4, 5, 6, 7, 8, 12, 14, etc.) by the coxal suture *l*, which is merely a ventral extension of the pleural suture *g*, prolonged downward into the coxal region. The anterior region *vc* has been termed the veracoxa (Crampton, 1914) or coxa genuina (Walton, 1900) and the posterior region may be termed the merocoxa, or simply the meron (Walton, 1900).

In the upper region of the veracoxa *vc*, there frequently occurs a narrow marginal sclerite *cm* (Figs. 2, 3, 8, 10, etc.). In the Trichoptera (Fig. 6) the region *cm* has been mistaken for the trochantin; but the true trochantin is contained in the compound sclerite *ptn*, which articulates with the coxa. The region *cm* is usually small and unimportant.

The veracoxa *vc*, or anterior subdivision of the coxa, may become immovably united with the lower portion of the pleural plate, as in certain Diptera (Fig. 11). Under these conditions, the loss of movement in the coxa is usually compensated by the breaking off of small movable plates called "coxites" (Fig. 11, *cxi*). The largest "coxite" frequently bears a spine-like process the coxal spine, as shown in Fig. 11.

From its close connection with the epimeron in higher insects, such as the Diptera, Lepidoptera, and Trichoptera, the meron *me* (of all figures), or posterior subdivision of the coxa, has been regarded by some investigators as a detached portion of the epimeron, which has become adherent to the coxa. This derivation of the meron, however, merely reverses the true evolutionary sequence, for in the lower pterygote insects, such as the Blattoidea (Fig. 2), the meron is clearly a portion of the coxa, and the suture which demarks it from the remainder of the coxa is but incompletely developed in these insects. In the Isoptera (Fig. 3) the meron is distinctly demarked from the remainder of the coxa; but it is still clearly a portion of the coxa, and is widely separated from the epimeron. It is only in the higher insects that the meron becomes smaller, and migrates upward toward the lower portion of the epimeron, as shown in Figs. 5, 13 and 14. On this account, it is far more reasonable to suppose that the meron is a demarked region of the coxa, than that it is a detached portion of the epimeron which has become adherent to the coxa, and the terms veracoxa and merocoxa have been applied to the two subdivisions of the coxa, in order to emphasize the fact that both are merely portions of the coxa itself.

The tendency of the meron to migrate upward toward the lower region of the epimeron, is clearly shown in the Trichoptera (Fig. 5); and in the thorax of *Mantispa* (Fig. 13) the meron, *me*, is very closely connected with the lower portion of the epimeron, *hem*. In the lower Diptera, such as the Tipulidae, the meron, *me*, (Fig. 14) occupies the normal position with reference to the anterior region of the coxa, *vc*, and the lower portion of the epimeron, *hem*, yet practically everyone who has figured these insects interprets the region *me*, as the "posterior portion of the sternum". To anyone studying the series of insects figured in the accompanying plates, however, it will be quite obvious that the region *me* of Fig. 14, occupies the position characteristic of the meron of other insects. When the coxal region is spread out as in Fig. 15, it can be readily seen that the sclerite *me* of the Tipulidae, is not connected with the sternum at all, but is closely united with the remainder of the coxa *vc*, from which it is demarked by the suture *l*, which is a ventral prolongation of the pleural suture *g*, as in all other insects. Furthermore, the same muscles which are attached to the meron in other insects, are attached to the region *me* in the Diptera (Figs. 14 and 15); so that the only logical conclusion to be drawn from a thorough study of the region in question, is that it is homologous with the meron of other insects. This fact seems so very evident, that it is difficult to understand how that anyone could have arrived at any other conclusion.

The fact that the meron *me* has completely fused with the epimeron *em*, in the mesothorax of *Panorpa* (Fig. 4) indicates a tendency on the part of the meron to unite with the lower portion of the epimeron in the higher insects; and the migration of the meron upward toward the pleural region in certain insects (Figs. 5, 13, etc.) has already been pointed out. It is therefore not surprising to find that in the higher Diptera, the meron has migrated up into the pleural region, and has united with the lower portion of the epimeron, to form the region designated as *mpl*, in Fig. 11. The region *mpl* of Fig. 11 corresponds roughly to the fusion product of sclerites *me* and *hem* in Figs. 13 and 14. On this account, the region *mpl* of the higher Diptera (Fig. 11) has been designated as the meropleurite (Crampton, 1914) to indicate that it is the fusion product of the meron and lower portion of the pleural region.

Those who interpret the region *mpl* of Fig. 11, or the sclerite *me* of Fig. 14, as the "posterior portion of the sternum", regard the

region *spl* of Figs. 11 and 14, as the "anterior portion of the sternum", and likewise interpret the region *aes*, of Figs. 11 and 14, as the entire episternum. If we compare together Figs. 14 and 13, however, it is at once apparent that the region *aes* of Fig. 14 is homologous with the region designated as *aes* in the Neuroptera (Figs. 13 and 8); and it has already been shown that the region *aes* of Figs. 13 and 8 is not the entire episternum, but is merely the upper portion of the episternum which becomes marked off in the roach (Fig. 2, *aes*) and other lower insects. In the same way, by comparing Figs. 14 and 13 together, it is evident that the region designated as *spl* in Fig. 14 is homologous with the compound region *spl* of Fig. 13. In other words, it is the lower portion of the episternum, etc. united with the sternum. The region *spl* (Figs. 14 and 11) has been called the "sternopleura" by Dipterologists, and this designation (slightly modified to sternopleurite) should be retained for the region in question.

In the metathorax of the beetle *Dytiscus*, a posterior region *m* (Fig. 24) is marked off in the coxa. This posterior region, while not strictly homologous with the meron of other insects (i. e. *me* of all figures), corresponds in a general way to the meral region. Audouin, 1824, who introduced the term trochantin, applied this term to the region *m* of Fig. 24, in his figures of *Dytiscus*, and Audouin likewise states that the trochantin articulates with the epimeron, instead of with the episternum, although in some cases he later correctly identified the true trochantin. Audouin's unfortunate mistake of applying the term trochantin to the region *m* (Fig. 24) in *Dytiscus*, is doubtless responsible for the incorrect designation of the meron as the "trochantin", by the earlier writers.

The trochanter.

The trochanter, *tr* (of all figures) is always more closely connected with the femur *fe*, than with the coxa, and is considered by some investigators as a "constricted-off" portion of the femur. In the Phasmids it is very closely united with the femur, and in the metathorax of the grasshopper (Fig. 16) it is immovably united with the femur, though demarked from it by a distinct suture. It is doubtless due to the fact of its close union with the femur in the metathorax of the grasshopper, that the trochanter of the metathoracic leg was overlooked by the earlier writers, who designated the true coxa *cx*

(Fig. 16) as the "trochanter", and interpreted the membranous region between the true coxa and the pleural region, as the "coxa".

The femur may be broadley joined to the apex of the trochanter (in which case, the line of union is transverse) or the femur may be joined to the side of the trochanter (in which case the line of union is oblique). These features are made use of in the classification of the Coleoptera, and other insects.

In the Myrientomata (Fig. 20) among the Apterygota, and in the Plecoptera (Fig. 21) among the Pterygota, the trochanter, *tr*, is reduced to a narrow ring above the femur. In some insects, the trochanter may be broader than long, while in others it is longer than broad. In the Carabidae, it is unusually large and well developed.

In certain Hymenoptera, designated as the Ditrocha, the so-called trochanter consists of two parts, a proximal and a distal trochanter (Fig. 23, *ptr* and *dtr*). The distal trochanter *dtr* is always very closely connected with the femur, and is considered by many as a portion of the femur demarked by a constriction, while others regard it as a portion of the trochantin, which itself may be a "constricted-off" portion of the femur. In the larvae of certain Odonata (*Agrion*) the trochanter appears to be marked off into two regions, and indications of a similar demarkation occur in the larvae of certain Coleoptera (*Dytiscus*) and Trichoptera (*Ithytrichia*). A small proximal region (not shown in Fig. 18) is marked off in the trochanter of *Machilis*, but this does not seem to be entirely homologous with the proximal region of the trochantin described in the above mentioned insects. The views as to the homologies of the trochanter in different arthropods will be discussed in the second part of this paper.

Interpretations of other investigators.

One of the most important of the earlier works dealing with homologies of the parts of the leg of an insect, as compared with those of other arthropods, is the article by Hansen, 1893. According to Hansen, the trochantin (or the "pseudo-trochantin") of an insect, is homologous with the coxopodite of the leg of a crustacean, while the insect's coxa would be homologous with the crustacean's basipodite, etc. Henneguy, 1904, however, proposes the method of comparison given in the appended table.

Insect	Crustacean
Coxa	Coxopodite
Trochanter	Basipodite
Femur	First segment of endopodite
Tibia	Second segment of endopodite
Tarsus	Remainder of endopodite

Since Henneguy believes that the coxa of an insect is homologous with the coxopodite of a crustacean, he maintains that the styli, or appendages borne on the meso- and metathoracic coxae of *Machilis* (Fig. 18), correspond to the epipodite (i. e. the appendage of the coxopodite) of the Crustacea. Hansen, 1893, however, together with Jourdain, 1888, and Wood-Mason, 1879, considers that the styli represent the exopodite of the Crustacea. Haase, 1889, regards the styli as cuticular appendages belonging in the same category with the tibial spurs, and other cuticular appendages. Banks, 1893, is of the opinion that the styli represent the vestigeal legs of a second subsegment which enters into the composition of the typical thoracic segment; but this view is entirely fanciful, and the same may be said of those theories in which it is maintained that the abdominal styli represent vestigeal legs. A comparison of the parts of an insect's leg, with those of the legs of other arthropods, has been made by Boerner, Grünberg, Silvestri, Verhoeff, and Walton, whose writings are listed in the appended bibliography.

Miall & Denny, 1886, have suggested that the trochantin and the pleural sclerites of the roach are "two basal leg joints which have become adherent to the thorax". Heymons, 1889, has likewise come to a somewhat similar conclusion from his study of the embryos of certain Hemiptera. Thus, he states that while the epimeron (which he designates as the "pleurit") of the nymph of *Nepa*, is in no wise connected with the leg region, from the embryological standpoint, the „subcoxa", on the other hand (i. e. the episternum together with the pre-coxal bridge connecting it with the sternum) is in reality the basal portion of the leg.

In attempting to compare these parts of the thorax of *Nepa*, with the sclerites of the Blattidae, Heymons comes to some very remarkable conclusions. Thus, he regards the "subcoxa" (i. e. the episternum and the pre-coxal bridge connecting it with the sternum) of the mesothorax of *Nepa*, as the representative of both episternum and epimeron of the mesothorax of the Blattidae; and he then comes

to the remarkable conclusion that the the epimeron of the mesothorax (which he terms the "pleurit") of *Nepa*, represents both the episternum and epimeron of the metathorax of the Blattidae. The mesothoracic epimeron of *Nepa* is thrown into a fold by the forward shifting of the region behind it, and overlaps the metathoracic epimeron, which escaped Heymons' attention entirely, although it may by readily seen upon raising the flap-like fold of the mesothoracic epimeron.

There is such a flattening, shifting, and distortion of the sclerites in the insects upon which Heymons bases his conclusions, that he was completely deceived as to the interpretation of these sclerites, thus illustrating how easy it is to be misled in dealing with the ill-defined sclerites of the embryo. On this account there would seem to be considerable ground for doubt as to whether the region which Heymons terms the "subcoxa" is really a basal portion of the leg, or is merely a portion of the pleural region, which in the embryonic stages it not clearly demarked from the leg region; for the leg is closely connected with the pleuron in the embryonic stages, and the sutures which demark the sclerites are not usually apparent in the early stages of development.

It will be at once apparent to anyone who will glance at Heymons' figure of the thorax of *Nepa*, that the region which he designates as the "subcoxa", is merely the episternum, together with the pre-coxal bridge connecting it with the sternum. As a result of Heymons' mistake concerning the homologies of the "subcoxa" in other insects, however, there has been a great deal of speculation as to what plate should be designated as the subcoxa in insects in general. Thus, Boerner states that the subcoxa is the equivalent of his "merosternum", while Verhoeff maintains that it is equivalent to his "coxopleure" together with the trochantin, and Enderlein claims that it is the trochantin alone. Prell applies the term subcoxa to the "pseudo-trochantin" of the Myrientomata, apparently using the term subcoxa as a synonym of trochantin. Berlese and many other recent investigators have adopted Enderlein's method of applying the designation "subcoxa" to the trochantin, although there is no apparent advantage to be gained by so doing. The term trochantin (or trochantinus) has been applied to the sclerite in question by entomologists the world over, for the past ninety years, and is understood by everyone. It thus has everything to recommend it, while the term subcoxa is not even appropriate, for

the trochantin is supra-coxal (i. e. above, or dorsal to the coxa) and is therefore not sub-coxal (i. e. below, or ventral to the coxa) in position! Furthermore, it is extremely doubtful that the trochantin is a basal portion of the leg, as is maintained by those who term it the "subcoxa", and as is implied by the latter designation. On this account, the application of the term "subcoxa" to the trochantin, is not only useless, but misleading.

Of the varied and heterogeneous collection of sclerites to which Berlese, 1909, applies the designation "subcoxe o trochantini", only the plate which he terms the "subcoxe" in his fig. 197 of *Acridium* (i. e. the plate labeled *sc* in Fig. 16, of the present paper) is appropriately designated, since it is the only one situated ventral to, or below the coxa (i. e. is sub-coxal in position). This sclerite, however, is merely a region of the sternum, and is not at all homologous with the plate which Berlese calls the "subcoxe o trochantini" of the meso- and metathorax in his fig. 196 of *Gryllus* (i. e. a plate homologous with the plate designated as *lst* in Figs. 3 and 19, of the present paper). Furthermore, the plate which Berlese terms the "subcoxe o trochantini" in his fig. 185 of the thorax of *Cicada* (i. e. *tn* of Figs. 10 and 12 of the present paper) is not homologous with either of the above mentioned sclerites. It is apparent that the term subcoxa cannot be applied to all of these different sclerites without creating confusion, so that it is preferable to restrict the term subcoxa to the episternum, together with the pre-coxal bridge connecting it with the sternum, as was done by Heymons, 1889 (who introduced the term subcoxa), and to apply the term trochantin only to the sclerite so designated in the present paper.

Jordan, 1902, considers that the upper marginal region of the coxa, *cm* (Fig. 6) in certain Trichoptera, represents the trochantin. The trochantin, however, is included in the region designated as *ptn* in Fig. 6, since this region includes the projection articulating with the coxa, while the marginal region *cm* of Fig. 6, is merely the upper portion of the veracoxa, *vc*, and is homologous with the sclerite designated as *cm* in Figs. 9, 8, 3, 2, etc.

The composite region *ptn* of Fig. 8 (of *Corydalis*) is designated as the trochantin alone by Snodgrass, 1909, who is consequently forced to assume that the small plate *aes* (Fig. 8) represents the entire episternum (*es*, of Figs. 1, 2, 3, etc.). It has already been shown, however, that the homologue of the episternum always extends from the top to the bottom of the pleural plate, so that the sclerite

acs is merely the upper portion of the episternum, while the lower portion of the episternum has united with the trochantin and the narrow marginal region called the antecoxale (*ac* of Figs. 1 and 2) to form the composite region *ptn* of Fig. 8.

Lowne, 1890—1892, likewise homologizes a portion of the episternum (which he designates as the "epitrochlea") with the trochantin, in the prothorax of the blowfly. He is mistaken, however, in his statement that this "epitrochlea is certainly the trochantin of Audouin and the rotula of Straus Durckheim", for his "epitrochlea" corresponds in part to the prothoracic episternum.

Comstock & Kochi, 1902, consider that the posterior region of the trochantin designated as *pt*, in Fig. 2 (of the present paper) represents the entire trochantin in the meso- and metathorax of the roach, and that the anterior region of the trochantin, *at*, represents the "antecoxal piece". The designation „antecoxal piece", however, is always applied by other writers, to the sclerite *ac* (Fig. 2, and 1) in the roach, as is done by Walton, 1900, although this sclerite is not strictly homologous with the so-called "antecoxal piece" of the Coleoptera, which is a sternal subdivision. The true antecoxal piece, or antecoxale, *ac*, of the roach (Fig. 2) is termed the "second antecoxal piece" by Comstock & Kochi. The terms "antecoxal piece" and "second antecoxal piece", would imply that the two sclerites were either parts of the same plate, or at least had points in common, but the sclerites *ac* and *at* (Fig. 2) have nothing whatsoever in common, since *at* is the anterior portion of the trochantin *tn* (compare with Fig. 3), while *ac* is the posterior marginal region of the pre-coxal bridge connecting the episternum with the sternum. It is therefore preferable, if confusion is to be avoided, to restrict the designation „antecoxal piece" (or antecoxale) to the sclerite *ac* (Figs. 1 and 2) as is done by other writers and to term the anterior region of the trochantin, *at*, the anterior trochantin, or antetrochantin (instead of designating it as the "antecoxal piece") while the posterior region of the trochantin *pt*, instead of being designated as the entire trochantin, should be termed the posterior trochantin, or the postrochantin.

In his fig. 120 of the prothorax of the roach *Blabera* (which he uses to illustrate the sclerites of the Blattidae) Sharp, 1895, designates the true epimeron (*em* of Fig. 1, of the present paper) as a "fold of the pronotum", while the basal portion of the entire trochantin (i. e. *bt*, of Fig. 1), he thinks is the "epimeron", and the

detached distal portion of the trochantin *tnl* (of Fig. 1), he designates as he entire trochantin. Verhoeff, 1902, and Snodgrass, 1908—1909, have followed Sharp in designating the detached distal portion of the trochantin, *tnl* (Fig. 1) as the entire trochantin, in the prothorax of the roach, but they regard the basal region of the trochantin *bt* (Fig. 1) as a portion of the episternum, instead of interpreting it as the epimeron (as was done by Sharp). A careful study of the trochantin in all three thoracic segments, however, clearly shows that the region *bt* (Fig. 1) is the basal portion of the prothoracic trochantin, and that the plate *tnl* (Fig. 1) is the detached distal portion of the trochantin, instead of being the entire trochantin, as others would interpret it.

Audouin's erroneous statement that the trochantin articulates with the epimeron (instead of articulating with the episternum, as is actually the case) and the fact that Audouin, 1824, labeled the posterior region of the metathoracic coxa as the "trochantine", in his figure of the sclerites of *Dytiscus*, is apparently responsible for the mistaken designation of the posterior portion of the metathoracic coxa (*m*, of Fig. 24, of the present paper) as the "trochantin", by Comstock, 1913, in his fig. 611 of the beetle *Enchroma*. The same misleading statement of Audouin's is apparently responsible for the fact that Packard, 1898, designates the meron of the meso- and metathoracic coxae as the "trochantine", in his fig. 90, of the thorax of the moth *Telea*, although Packard may have been influenced in this matter, by the fact that Westwood, 1832, in his figure of *Telea* (tab. 121) designates the meron of this insect as the "trochantine".

In his fig. 89 of *Melanoplus*, Packard designates the posterior portion of the pro- and mesothoracic coxae as the "trochantine", and likewise applies the term trochantine to the membranous region between the true coxa (called the "trochanter" by Packard) and the pleural region, in the metathorax of this insect. It is unfortunate that this misinterpretation of the sclerites has not been noted or rectified before, since Packard's figure of the grasshopper has been widely adopted, to illustrate the anatomy of this insect.

Newport, 1839, applied the term trochantin, to the anterior portion of the coxa (or to the veracoxa, *vc*, when the latter is clearly marked off from the remainder of the coxa), and restricts the designation coxa, to the posterior portion of the coxa (or to the meron, when the latter is clearly demarked from the remainder of the coxa). Packard, 1883, was apparently influenced by Newport's

ideas concerning the intrepretation of the parts of the coxa, in his earlier work, for in the paper published in 1883, Packard usually designates the anterior portion of the coxa (or the veracoxa) as the "trochantine"; and restricts the term coxa to the posterior portion of the coxa (or to the meron), thus reversing the order which he uses in his later work, in which he applies the term coxa to the anterior portion of the coxa, and the term trochantine to the posterior portion of the coxa. In some insects, such as *Corydalis*, Packard, 1883, calls the meron, the "infra-epimerum" (see tab. 64, figs. 2 and 3, of Packard's work), apparently not recognizing the true nature of the sclerite in question, in the different insects. Indeed, Packard has hopelessly confused the homologies of the sclerites in his earlier work, and his figures are frequently so inaccurate as to make it extremely difficult to determine exactly what sclerite he intended to portray. In general terms, however, it may be said that he regarded the true trochantin as one of the three subdivisions of which he thought the episternum is composed (e. g. as in his fig. 13, tab. 32, of the thorax of the roach *Periplaneta*).

It is possible that the fact that Packard, 1883, designated the meron as the "infra-epimeron" in such insects as *Corydalis*, may have given rise to the idea that the meron is a detached lower portion of the epimeron, which has become adherent to the coxa. At any rate, Kolbe, 1893, who terms the meron a "stützendes Hüftstück" (i. e. a supporting coxal piece) in his fig. 168 of the hind leg of *Panorpa*, states that it appears to be a process of the epimeron, which has become demarked from the remainder of the epimeron, by the formation of a suture. Kolbe, however, expressly states that this "stützendes Hüftstück" is different from the "Hüftangel" or trochantin, while Sharp, 1895, who likewise designates the meron as a "coxal fold of the epimeron" in his fig. 58, of the hind leg of *Panorpa*, states that it "may possibly be the homologue of the the trochantin of some insects". Snodgrass, 1909, likewise maintains that the meron is a detached portion of the epimeron, which has become adherent to the coxa, on the ground that in the pupal stages of *Corydalis*, the meron is not sharply demarked from the epimeron, but becomes first marked off in the adult stage. To this argument, it might be replied that in the far more primitive forms, such as the Blattidae, the meron is clearly a portion of the coxa, and is distinctly separated from the epimeron. It is imper-

fectly demarked from the remainder of the coxa in the early stages of development in the Blattidae, thus clearly showing that it is merely a demarked posterior region of the coxa in these lower insects, while in the higher forms, such as the Panorpidae and Diptera, the meron becomes secondarily united with the epimeron. On this account, it would be merely reversing the evolutionary sequence to regard the meron as a detached lower portion of the epimeron which has become adherent to the coxa, rather than to regard it as a posterior region of the coxa which has become closely attached to the epimeron in the higher insects. In order to emphasize the fact that the meron is merely a portion of the entire coxa, we have proposed the term merocoxa for the region in question, while the anterior portion of the coxa is designated as the veracoxa.

In the lower Diptera, such as the Tipulidae (Figs. 14 and 15), the meron *me*, occupies the characteristic position with reference to the remainder of the coxa, and the same group of muscles are attached to it as are attached to the meron in other insects, yet Brauer, 1882, calls the meron of the mesothoracic coxae, the "metasternum", apparently being misled by Westwood, 1832, who makes a similar mistake in his figure of *Tipula* (tab. 122). Snodgrass, 1909, likewise regards the meron as the posterior region of the sternum (but of the mesothorax instead of the metathorax) in the lower Diptera, and Berlese, 1909, has the same idea concerning the meron of the Lepidoptera, since he terms it the "sternello" (i. e. sternellum) in his fig. 182 and 183 of *Sphinx*.

In the higher Diptera (Fig. 11) the meron has united with the lower portion of the epimeron to form the composite region *mpl*, which is invariably misinterpreted by all Dipterologists. Thus Hammond, 1880, regards it as the entire epimeron; Petri, 1899, terms it the poststernum (i. e. the posterior region of the mesosternum); Snodgrass, 1909, designates it as the posterior portion of the sternum (of the mesothorax); Westwood, 1832, Kuenkel d'Herculais, 1875—1881, Brauer, 1882, Lowne, 1890—1892, Packard, 1898, Hewitt, 1907—1910, and many others, regard this mesothoracic region (i. e. *mpl* of Fig. 11) as the sternum of the metathorax; and Osten-Sacken, 1884, together with Williston, 1908, and many recent Dipterologists, apparently regard it as a portion of the metathorax, which they designate as the "hypopleura". A study of the musculature, however, and a comparison of the sclerites in a series of intermediate forms, clearly shows that the region *mpl*

(Fig. 11) is merely the mesothoracic meron united with the lower portion of the mesothoracic epimeron, and is therefore neither metathoracic, nor sternal. On this account, the term meropleurite (Crampton, 1914) has been here retained for the region in question, to indicate that it is the meron together with a portion of the pleuron (lower portion of the epimeron).

As may be seen from the foregoing discussion, the meron has been intrepreted in the most varied and astonishing fashion in different insects, by different entomologists, and various designations from the "pesella" (applied to the meral spur in the metathorax of the Cicadas, *me*, of Fig. 12) of Kirby & Spence, 1828, to the meron of Walton, 1900, have been applied to it. Walton terms the anterior region of the coxa, *vc*, the "coxa genuina", but it is preferable to designate it by a single term such as eucoxa or veracoxa (Crampton, 1914), and to term the meron the "merocoxa", if it is desirable to indicate that it is a portion of the coxa.

Walton's idea that the meron represents the vestigeal leg of a second subsegment entering into the composition of the meso- or metathorax is, of course, purely fanciful, since there is no evidence, embryological or otherwise, that each segment is composed of two fused subsegments; and Banks' theory that the styli, borne on the meso- and metathoracic coxae of such insects as *Machilis*, represent the vestigeal legs of a second subsegment, belongs in the same category.

Kirby & Spence, 1826—1828, Vol. 3, p. 579 confuse the posterior coxae of *Dytiscus*, with the metasternum. It would appear that they have taken this idea from De Geer, since the footnote to p. 579, in which they refer to "De Geer iv. t. iv. f. 3. dd. ee." apparently has reference to this usage by De Geer, although the work in question is not accessible to us for determining this point.

As was mentioned above, Packard, 1898, terms the metathoracic coxa of the grasshopper, the "trochanter". It is doubtful, however, that in so doing he was influenced by the fact that in the prothorax of *Tipula* (tab. 122) Westwood, 1832, applies the term "trochanter" to the coxa. It would appear that Westwood did not appreciate the true nature of the trochanter, since he applies this term to the veracoxa in the mesothorax of *Tipula* and *Telea* (tab. 122 and 121).

Langer, 1860, regards the trochanter as an "epiphysis" of the femur, and Gerstaecker suggested that in the Hymenoptera Ditrocha,

the distal trochanter is a portion of the femur demarked by a constriction, and VERHOEFF, 1902, arrived at the same conclusion from his study of the musculature. VERHOEFF considers that the distal region of the trochanter of insects (which he terms the praefemur) is the homologue of the femur of Chilopods, while the proximal region of the trochanter of insects, he thinks represents the true trochanter. This view, however, is combatted by GRUENBERG and BOERNER. GRUENBERG interprets the division of the trochanter into two regions in the Odonata, etc., as the result of the formation of an internal ridge for the stiffening of the trochanter, and states that the two regions thus formed in the trochanter of the Odonata are not strictly homologous with the two subdivisions of the trochanter of such insects as *Machilis*.

According to BORDAGE, 1898, the trochanter was originally a distinct segment in the ancestors of the Phasmids, but, due to the stress and strains experienced by these insects in the process of moulting (during which the legs are frequently pulled off) the region between the trochanter and femur became hardened and more strongly chitinized, leaving merely a constriction demarking the trochanter from the femur. It is impossible, however, in the present state of our knowledge concerning it, to decide as to the correctness of these theories concerning the nature of the trochanter.

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Explanation of Plate.

The subscripts *1*, *2*, and *3*, denote that the sclerite in question belongs to the pro-, meso-, or metathorax.

a Pleural fulcrum of the coxa
ac Antecoxale, or antecoxal piece
aes Anepisternum, or upper region of episternum
at Antetrochantin, or anterior region of trochantin
b Apex of trochantin
bt Basitrochantin, or basal portion of trochantin
c Sternal fulcrum of coxa
cm Coximarginale, or marginal region of coxa
cx Coxa
cxi Coxite, or detached plate of coxa
dtr Distal trochanter
em Epimeron
es Episternum
fe Femur
g Pleural suture
hem Hypoepimeron, or lower region of epimeron
ip Interpleurite
jc Juxtacoxale
l Coxal suture
lpl Lateropleurite
lst Laterosternite
m Posterior region of coxa, not strictly homologous with meron
me Merocoxa, or meron
mpl Meropleurite, or fusion product of meron and lower portion of epimeron
per Pericoxale, or pericoxal ring
ppl Pteropleurite, or upper region of epimeron

pst Pseudo-trochantin
pt Posttrochantin, or posterior portion of trochantin
ptn Pleurotrochantin, or fusion product of lower portion of episternum, etc. with the trochantin. It is also called katepisternum
ptr Proximal trochanter
sc Sternocoxale
sl Sternal lobe (lobisternite)
spl Sternopleurite
st Sternum
stg Styliform appendage of coxa
tn Trochantin
tnl Trochantinelle, or detached distal portion of trochantin
tr Trochanter
vc Veracoxa, or anterior region of coxa

Plate 1.

Fig. 1. Prothorax of a Blattid (*Periplaneta*), lateral view.
Fig. 2. Mesothorax of a Blattid (*Ischnoptera*), lateral view.
Fig. 3. Mesothorax of a Termite (*Termes*), lateral view.
Fig. 4. Mesothorax and metathorax of a Panorpid (*Panorpa*), lateral view.
Fig. 5. Metathorax of a Trichopteron (*Halesus*), lateral view.
Fig. 6. Mesothorax of a Trichopteron (*Halesus*), lateral view.
Fig. 7. Metathorax of a Lepidopteron (*Anosia*), lateral view.
Fig. 8. Mesothorax of a Neuropteron (*Corydalis*), lateral view.

Plate 2.

Fig. 9. Mesothorax of a Neuropteron (*Corydalis*), ventral view.
Fig. 10. Mesothorax of a Cicada (*Cicada*), lateral view.
Fig. 11. Mesothorax and metathorax of a Syrphid (*Spilomyia*), lateral view.
Fig. 12. Metathorax of a Cicada (*Cicada*), lateral view.
Fig. 13. Mesothorax of a Neuropteron (*Mantispa*), lateral view.
Fig. 14. Mesothorax and metathorax of a Tipulid (*Tipula*), lateral view.
Fig. 15. Mesothoracic coxa of a Tipulid spread out to show relation of parts, lateral views.

Plate 3.

Fig. 16. Metathorax of an Acridid (*Rhomalea*), ventral view.
Fig. 17. Mesothorax of an Acridid (*Rhomalea*), ventral view.

Fig. 18. Mesothoracic leg of *Machilis*, based on figure by Verhoeff, 1902.

Fig. 19. Mesothorax of a Forficulid ventro-lateral view.

Fig. 20. Mesothorax of *Eosentomon*, based on figure by Prell, 1913.

Fig. 21. Prothorax of a Perlid (*Perla*), lateral view.

Fig. 22. Metathorax of a Forficulid lateral view.

Fig. 23. Metathoracic leg of an Ichneumon, lateral view.

Fig. 24. Metathorax of *Dytiscus*, ventral view.